

**Infrared detection in three pyrophilous beetles:
Melanophila acuminata, *Merimna atrata*, and *Acanthocnemus nigricans***

Gretchen Jehle

jehle@lamar.colostate.edu

Numerous insects are attracted to recently burned forests, presumably to exploit the abundant resource of freshly killed and weakened trees. The ability to quickly and accurately locate forest fires would therefore be expected to have adaptive value for some insect species that feed on or develop in burned trees. Organs capable of detecting infrared (IR) radiation have been identified in three beetle species (2 in the family Buprestidae and 1 in Acanthocnemidae). The most well-known of these is *Melanophila acuminata*, a flat-headed, wood-boring buprestid beetle whose behavior and physiology suggest that the species is dependent upon fire for persistence. *M. acuminata* have been frequently observed at forest fires, and also occasionally at large industrial fire sources, apparently in search of breeding grounds. Several researchers contend that the larvae of *M. acuminata* are only able to develop in burned trees. Mating often occurs while the fire is still burning and females deposit their eggs immediately after the fire has gone out. *M. acuminata* possess 2 metathoracic IR pit organs which have demonstrated sensitivity to IR emissions in the same range as forest fires. Their IR pit organs are assumed to be used for detecting forest fires over great distances, although the precise distance remains unconfirmed. Infrared receptors with similar sensitivities but different structures have recently been discovered in two beetles endemic to Australia (*Merimna atrata* and *Acanthocnemus nigricans*). Both of these beetles have demonstrated an affinity to fire, but neither is as well-studied as *Melanophila acuminata*. Although all three of these species have receptors for detecting infrared radiation, the morphology and physiology of each is distinct. The pyrophilous behaviors of each of these species will be reviewed, and the similarities and differences between their infrared detecting organs will be evaluated.

INTRODUCTION

A variety of insects are commonly observed in recently burned forests, presumably to exploit the abundant resource of freshly killed and weakened trees (McCullough et al., 1998). Because living trees have ample defenses to protect them, these dead or dying trees are easier for insects to exploit (Graham, 1939; Furniss and Carolin 1977). The

ability to quickly and accurately locate forest fires would therefore be expected to have adaptive value for insect species that feed on or develop in burned trees.

In North America, species commonly observed during or immediately after forest fires include longhorned beetles (Coleoptera, Cerambycidae), particularly members of the genus *Monochamus*; wood wasps (Hymenoptera, Siricidae); and metallic wood boring beetles (Coleoptera, Buprestidae) which includes the well-studied species *Melanophila acuminata* (Evans, 1966b; Leatherman, 2002; McCullough et al., 1998). During the first few years post-fire, a variety of bark beetles are frequently observed in burned conifers, including members of the *Ips* and *Dendroctonus* genera (McCullough et al., 1998; Leatherman, 2002). In Australia, two beetle species that are affiliated with fire are *Merimna atrata*, and *Acanthocnemus nigricans* (Poulton, 1915; Champion, 1922; Schmitz et al., 2000b; Schmitz et al., 2002).

Specialized sensilla capable of detecting infrared radiation have been identified in three pyrophilous beetle species *Melanophila acuminata*, *Merimna atrata*, and *Acanthocnemus nigricans* (Evans, 1964; Schmitz et al., 2000b; Schmitz et al., 2002). The morphology and physiology of the IR organs is distinct for each of these species, and recent research has scrutinized the similarities and differences between all three types (Schmitz et al., 2002). Most research to date has focused on *Melanophila acuminata* and other congeneric species. This review will provide a synopsis of the behavioral, morphological, and physiological research examining *Melanophila acuminata* as well as recent work investigating the form and function of infrared receptors in *Merimna atrata*, and *Acanthocnemus nigricans*. Finally, suggestions for future research will be provided.

MELANOPHILA ACUMINATA

Melanophila acuminata is a flat-headed, wood-boring buprestid beetle distributed throughout the holarctic region and also in parts of the nearctic region (Burke, 1919; Sloop, 1937). *Melanophila* species have large-headed larvae (see Figure 1), and usually breed in dead or dying coniferous trees (Sloop, 1937; Furniss and Carolin 1977). Species of the *acuminata*-type are frequently observed near fire sources (Linsley, 1933; Linsley, 1943). *Melanophila* initiates the post-fire decomposition process by ovipositing in freshly killed trees, often while the forest is still burning (Evans, 1966b). *Melanophila acuminata* have two metathoracic pit organs containing sense organs (Sloop, 1937; Evans, 1966b; Schmitz et al., 1997; Vondran et al., 1995). Based on this morphological attribute, the genus *Melanophila* was reclassified in 1937 and a subgenus *Melanophila* was designated to include only those species possessing these thoracic pit organs (*acuminata*-type, as opposed to *gentilis*-type); the other two subgenera were classified as *Phaenops* and *Xenomelanophila* (Sloop, 1937).

Figure 1. Larva of *Melanophila acuminata*, showing the enlarged head. Larvae of this species develop inside dead trees; when they burrow, they create galleries which initiate decomposition of the trees (Hart 1998).

DESIGNATION OF THE SUBGENUS *MELANOPHILA*

Seven North American *Melanophila* species (out of a possible 15) are contained in the subgenus *Melanophila*, including: *M. acuminata*, *M. consputa*, *M. notata*, *M. notata elegans*, *M. opaca*, *M. occidentalis*, and *M. atropurpurea* (Sloop, 1937; Furniss and Carolin 1977). Other species in the subgenus *Melanophila* include the palearctic species *M. unicolor*, and *M. cuspidate* and the neotropical species *M. atra* (Evans, 1966a). Species possessing these pit organs (*acuminata*-type, *Melanophila* subgenus) have been

observed flying to forest fires; those species lacking the sensory pit organs (*gentilis*-type) have not demonstrated this behavior, suggesting that these pit organs are correlated with pyrophilous behavior (Evans, 1966a; Linsley, 1933; Sloop, 1937).

BEHAVIORAL OBSERVATIONS: ATTRACTION TO FIRE

Reports of *Melanophila* beetles congregating at fire sources are abundant in the entomological literature (Ricksecker, 1885; Manee, 1913; Van Dyke, 1926; Linsley, 1933; Linsley, 1943; Evans, 1966b). Evans (1966) notes that “it is a common observation that species of *Melanophila* often inhabit a dead tree to the exclusion of other borers of freshly killed wood, indicating that they had completely occupied the tree before the other forms arrived.”

Ricksecker provides an early account in which he observed four *Melanophila* beetles in a burned spruce stump in the act of eating scorched termites, although buprestids are usually xylophagous rather than carnivorous (Ricksecker, 1885). In North Carolina, Manee learned that the native people referred to *Melanophila* beetles as “fire bugs” because they believed the beetles actually came from the fire. He speculated that the beetles were probably drawn to fire by the scent of burning pitch (Manee, 1913), an idea posited subsequently by others (e.g. Linsley, 1943), tested and rejected behaviorally (Evans, 1964), and still poorly understood (Schutz et al., 1999).

Van Dyke observed a large swarm of *M. consputa* at an oil fire in Coalinga, California, over 50 miles from the nearest coniferous forest which could have provided the source of the beetles (Van Dyke, 1926). This demonstrated that *Melanophila* beetles must be able

to detect fires from great distances, but the mechanism by which this was achieved was unknown.

Linsley observed both *M. consputa* and *M. acuminata* swarming at football games in Berkeley, California, and speculated that they may have been attracted to the smoke from approximately 20,000 cigarettes (Linsley, 1943). In his review, he summarized “the buprestid beetles of the subgenus *Melanophila* s.str. appear to be attracted over long distances by smoke from a variety of burning materials, including wood, oil, mill refuse, smelter products, and possibly tobacco. In nature, this attraction leads them to forest fires where they normally oviposit in scorched coniferous wood. The beetles are also stimulated by heat, and in the vicinity of the source they fly rapidly and run about over hot surfaces. Light probably plays little role in their attraction to fire.” (Linsley, 1943)

BEHAVIORAL EXPERIMENTS

To evaluate this attraction to fire, the Canadian entomologist William G. Evans performed a series of behavioral experiments on *Melanophila acuminata* (Evans, 1964; Evans, 1966a; Evans, 1966b; Evans and Kuster, 1980). Prior observers had suggested that olfactory cues may lead *Melanophila* beetles to fire (e.g. Manee, 1913; Linsley, 1943). Surprisingly, Evans observed no olfactory response of these beetles to smoke, carbon dioxide, or carbon during experiments using an olfactometer (Evans, 1964), but this result has recently been challenged (see Sensory Function of Antennae, below)

The pit organs had previously been recognized, but their exact function had not yet been determined. After experimentally eliminating the possibilities that these pit organs were olfactory, auditory, or proprioceptive, Evans discovered that the organs were capable of

detecting infrared radiation (Evans, 1964). The beetles responded to infrared radiation by twitching their antennae on the stimulated side (Evans, 1964). This was the first description of an infrared-detecting organ in an insect. Evans hypothesized that the paired IR organs would function tropotactically (when an animal has more than one sensory receptor, it can determine the location of a source by the magnitude of the stimulus at each receptor), for long-range orientation, and that thermoreceptors in the antennae would function for short-range orientation (Evans, 1964).

SENSORY FUNCTION OF ANTENNAE IN *MELANOPHILA ACUMINATA*

The lack of a behavioral response to olfactory stimulus has recently been contradicted by a physiological study, which showed that excised antennae from *Melanophila acuminata* reacted to volatiles generated by smoldering wood (Schutz et al., 1999). This is corroborated by Campbell et al. (2002), who report “although many studies provide evidence that *Melanophila* are attracted to forest fires solely by the detection of the emitted IR radiation and not by visual, auditory, or olfactory cues..., a recent study shows that they may be attracted to forest fires by a combination of olfactory cues and IR radiation (unpublished results)” (Campbell et al., 2002).

Furthermore, the antennae of female *Melanophila acuminata* were found to possess 20-30 campaniform-like organs whose function remains speculative (Scott and Gara, 1975). Antennae from male *M. acuminata* and from both sexes of *M. drummondi* (which is not a pyrophilous species) lack these organs. Due to the pyrophilous behavior of *Melanophila acuminata*, the researchers hypothesized that these sensilla may assist the female to

identify the optimal or threshold temperatures within the bark for oviposition of eggs (Scott and Gara, 1975).

PERCEPTION OF INFRARED RADIATION

The ability of *Melanophila acuminata* to detect forest fires using infrared receptors is facilitated by the convergence of three phenomena: (1) their IR receptors respond to wavelengths between 2.4 and 4.0 μm , with a maximum sensitivity at 3.0 μm (Evans, 1966b); (2) forest fires burn at temperatures between 435 and 1150° C, which corresponds to IR emission wavelengths in the range from 2-4 μm (Schmitz and Bleckmann, 1997); and (3) the atmosphere absorbs infrared radiation unevenly, with very little absorption between 3 and 5 μm (Hart, 1998). Because all three of these factors are maximized around 3 μm (highest sensitivity, greatest output, minimal interference), infrared radiation provides an ideal means for the detection of forest fires (Schmitz and Bleckmann, 1997; Schmitz and Bleckmann, 1998; Hart, 1998; Pain, 1999; Hammer et al., 2001b; Campbell et al., 2002; Hammer et al., 2002)

ESTIMATES ON DISTANCE OF DETECTION

The distance from which infrared radiation can be detected by *Melanophila* has been variously estimated to be: 1 km on flat terrain and 5 km for mountainous terrain (Evans, 1966b), 12 km (Schmitz and Bleckmann, 1998), 20 km (Linsley, 1943), 50 km (Gronenberg and Schmitz, 1999), and 80 km (Van Dyke, 1926). A recent study evaluating the sensitivity of the sensilla using electrophysiological techniques concluded that the detection limit is approximately 1 km (Hammer et al., 2001a).

A single study has assessed the sensitivity of the chemoreceptors in the antennae to smoke, estimating that “this sensitivity is sufficient for the beetle to detect a single pine tree 30 cm in diameter that has a smoldering bark to a height of 2 m ... under light wind conditions from a distance of more than 1km”(Schutz et al., 1999). Based on these findings, it remains unclear how *Melanophila* beetles are able to detect fire sources over great distances.

MORPHOLOGY OF INFRARED ORGANS IN *MELANOPHILA ACUMINATA*

The pit organs of *Melanophila acuminata* are located adjacent to the coxae beneath the legs on each side of the mesothorax (figures 2 and 7). These organs are exposed during flight, but concealed by the legs when walking. These paired pit organs contain 50-100 sensilla, depending on the size of the individual beetle (figure 3) (Evans, 1964; Evans, 1966a). Each sensillum consists of a spherule containing a single dendrite, and lacking an exocuticle (figure 4)(Vondran et al., 1995).

PHYSIOLOGY OF INFRARED ORGANS IN *MELANOPHILA ACUMINATA*

Recent work by Helmut Schmitz and his colleagues in Germany has further elucidated the morphology and physiology of these infrared organs (Gronenberg and Schmitz, 1999; Hammer et al., 2001a; Hazel et al., 2001; Schmitz and Bleckmann, 1997; Schmitz and Bleckmann, 1998; Schmitz et al., 1997; Schmitz et al., 2000a; Schutz et al., 1999; Sowards et al., 2001; Vondran et al., 1995).

Figure 2. From Schmitz & Bleckmann (1998)

Figure 3. From Hammer et al. (2001a)

Initial work focused on describing and classifying the sensilla within the pit organs (Vondran et al., 1995). Vondran et al. (1995) used scanning electron microscopy and transmission electron microscopy to examine the sensory pits and the sensilla within them. They confirmed that the pit organs lack an exocuticle and contain densely packed sensilla, each of which is associated with a wax gland (figure 3) (Evans, 1964; Evans, 1966a; Vondran et al., 1995). The wax glands presumably protect the sensilla from smoke, dirt, and desiccation (Evans, 1964; Evans, 1966a), and possibly reduce convective cooling of the sensilla during flight (Schmitz and Bleckmann, 1997).

Figure 4. From Hazel et al. (2001)

Each sensillum consists of a mesocuticular sphere, an endocuticular stalk, and an epidermal sensory neuron (figure 4) (Vondran et al., 1995). The sphere of each sensillum contains three distinct regions (1) a 6µm amorphous core; (2) a region of unstructured cuticle with irregular lacunae; and (3) an outer mantle of helical arranged cuticle (Vondran et al., 1995). Each sphere is innervated by a single, bipolar neuron, which consists of a 25-35 µm ciliary dendrite (Vondran et al., 1995). The dendrite has two segments, as shown in figure 4 above (DIS: dendritic inner segment and DOS: dendritic outer segment). The auxiliary cells associated with each neuron were tentatively named according to relative position and traditional nomenclature. Tormogen cells are the outermost cells which envelop the sensillum and secrete the cuticle; tricogen cells are in the middle and form the sensillum itself; and thecogen cells are the innermost cells, which form the dendritic sheath (definitions modified from Hallberg and Hansson, 1999). These infrared sensilla resemble and are surrounded by hair mechanoreceptors (sensilla tricoidea), from which they may have been derived (Vondran et al., 1995).

Schmitz and his colleagues hypothesized that the infrared sensilla of *Melanophila* operate via an unique photo-thermal-mechanical transduction mechanism, and further research has corroborated this idea (Schmitz et al., 1997; Schmitz and Bleckmann, 1998; Schmitz et al., 2000a; Schmitz et al., 2001; Hazel et al., 2001; Hammer et al., 2001a; Hammer et al., 2002). According to this hypothesis, when infrared radiation is absorbed by the cuticular spherule of the sensilla in the pit organs, the vibrational energy is converted into heat and causes a small change in the volume of the spherule (figure 5). According to their calculations, a change in volume of as little as 1nm is sufficient to deform the dendritic tip and trigger a nerve impulse (reviewed in Campbell et al., 2002).

When the sensitivity of the pit organs was evaluated, they responded to infrared radiation exclusively and showed no response to visible light, sound, or moderate air movements (Hammer et al., 2001a). This is consistent with the results of Evans' earlier behavioral experiments (Evans, 1964). The physiological and behavioral evidence demonstrate that the pit organs of *Melanophila acuminata* are adapted to detect infrared radiation.

Figure 5. Speculated transduction mechanism in the IR pit organ of *Melanophila acuminata*. Absorption of IR energy (large white arrow) causes thermal expansion of the spherule (small black arrows) and subsequent compression of the dendritic tip (small black arrowheads). DIS: dendritic inner segment; DOS: dendritic outer segment. Adapted from Hammer et al. (2002).

MELANOPHILA AND FIRE: PREFERENCE OR DEPENDENCY?

Helmut Schmitz and his colleagues repeatedly contend that *Melanophila* beetles strictly depend on fire because their larvae develop exclusively in burned trees (Vondran et al., 1995; Schmitz and Bleckmann, 1997; Schmitz et al., 1997; Schmitz and Bleckmann,

1998; Schmitz et al., 2000a;). In addition, subsequent authors have perpetuated the idea despite a lack of solid evidence (e.g. Campbell et al., 2002; Hart, 1998).

There is not strong support for the dependence of *Melanophila* on fire in the English-language scientific literature. The references frequently cited are Linsley (1943) and Graham (1939), but neither of those contains convincing data. In fact, Linsley (1943) cites Graham and summarizes that “living, uninjured trees are very resistant to successful attack by *Melanophila*, especially to *M. californica*” (Linsley, 1943). Graham provides little further evidence of a need for explicitly burned trees, stating “only when the tree is at the point of death are the larvae able to develop to maturity” (Graham 1939). There are certainly other ways for trees to be stressed “to the point of death;” fire is not the only mechanism for this.

According to Schmitz et al (2000), three German-language references (Apel, 1986; Apel, 1988; Apel, 1989) provide additional support for the idea that species of the subgenus *Melanophila* actually depend on fire. Schmitz further explains “it would not be so easy to make meaningful experiments which show that [*Melanophila*] larvae are unable to develop in unburnt (dead) wood. We are quite sure that larvae depend on burnt wood. In all regions of Germany, where forest fires are put out by the fire brigade immediately and the burnt wood is removed a few weeks after the burn, *Melanophila* is definitively extincted”(H. Schmitz, personal communication). There may also be additional evidence in Swedish (cited in Ehnstrom et al., 1995). These references merit further scrutiny. Unless the German or Swedish scientific literature cited above provides compelling

evidence, the dependence of *Melanophila* on fire should be considered hypothetical rather than confirmed.

PYROPHILOUS BEETLES IN AUSTRALIA

Infrared receptors have recently been discovered in two beetles endemic to Australia (*Merimna atrata* and *Acanthocnemus nigricans*) (Schmitz et al., 2000b; Schmitz et al., 2002). Both of these beetles have shown an affinity to fire, but neither has been studied as thoroughly as *Melanophila acuminata*. An early observer noted that *Merimna atrata* were called “fire beetles” because they were frequently observed close to actively burning brush (Poulton, 1915). *Acanthocnemus nigricans* has also been observed approaching forest fires and running around quickly close to the flames (Champion, 1922; Schmitz et al., 2002). There has been no investigation of whether either of these species requires or prefers burned resources for food or oviposition, but their association with fire has been established via observational evidence (Schmitz et al., 2000b; Schmitz et al., 2002).

COMPARING AND CONTRASTING IR ORGANS IN THREE BEETLE SPECIES

Although all three of the beetle species discussed in this review possess organs capable of detecting infrared radiation, the morphology and physiology of each is distinct. These differences are summarized in Table 1 and depicted in figures 6 and 7 below.

Table 1. Comparison of three beetles (Coleoptera) possessing infrared organs

| | Family | Distribution | Morphology of IR organs | Physiological response |
|--------------------------------|-----------------|--------------|-------------------------|--------------------------|
| <i>Melanophila acuminata</i> | Buprestidae | Holarctic | 2 mesothoracic | modified mechanoreceptor |
| <i>Merimna atrata</i> | Buprestidae | Australia | 4 ventrolateral | simple thermoreceptor |
| <i>Acanthocnemus nigricans</i> | Acanthocnemidae | Australia | 2 prothoracic | complex thermoreceptor |

Bar = 1 cmBar = 0.5 cm

Figures 6 and 7. Drawings of ventral views (legs removed) of *Merimna atrata* (left) and *Melanophila acuminata* (right) showing the location of the infrared organs on each (see black arrows). NOTE: drawings are in different scales. Adapted from Schmitz et al. (2000b) and Vondran et al. (1995) respectively.

Physiologically, the infrared organs of *Merimna atrata* act as simple thermoreceptors and can be best compared to the lip organs of boid snakes (Schmitz et al., 2000b). The infrared organs of *Acanthocnemus nigricans* also act as thermoreceptors, but their organs include an air-filled inner chamber, more closely resembling the organization of infrared organs in pit vipers (Schmitz et al., 2002). In contrast, the infrared organs of *Melanophila acuminata* are not thermoreceptors, but rather function as mechanoreceptors (see above in Physiology of Infrared Organs in *Melanophila acuminata*). It is intriguing that while all three of these beetle species have infrared detecting organs, each one is distinct in form and function.

SUGGESTIONS FOR FURTHER RESEARCH

The work by Schmitz and his colleagues built on the earlier work by Evans and has revealed much about the morphology and physiology of the IR organs in *Melanophila acuminata* and the receptors in the antennae. Much remains to be learned about how these two sensory systems function together in this species. According to Schutz et al. (1999) “It is unclear how the two sensory systems used by *Melanophila* to identify fire – the thoracic infrared receptors and the antennal olfactory receptors – act together to detect fire and orientate the beetle towards its source.”

Further behavioral research is needed to parse out how long-range detection of fire is achieved in these beetles, and how the IR organs assist with orientation towards fire. Several researchers have suggested that the IR organs may function tropotactically, but this has not been evaluated experimentally (Evans, 1966b; Schmitz et al., 2000a). Behavioral lab experiments could investigate if living beetles of these pyrophilous species orient towards or away from (1) smoke, (2) infrared radiation, or (3) other stimuli (e.g. similar to the work done by Moiseff et al. (1978) with crickets or Roeder (1965) with noctuid moths in response to acoustical stimuli).

Most of the research on *Melanophila* beetles has been performed on *M. acuminata*, with an implicit assumption that the findings hold for other congeneric species. Given the recent discovery of differences between the infrared organs in *Melanophila acuminata*, *Merimna atrata* and *Acanthocnemus nigricans*, investigation of the form and function of the sensilla in other *Melanophila* species is warranted.

The reasons why these beetle species prefer burned forests remain to be determined in terms of the ecological advantages conferred. Most of the research to date has focused on what stimuli these beetles detect and how they are able to detect them, with a general neglect of a possible rationale for their pyrophilous behavior based on nutrition, physiology, or enemy-free space.

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